Using ecological indicators in a whole-ecosystem wetland experiment

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Published as: pp 211-236 in: S.E. Jørgensen, R. Costanza, and F.-L. Xu, eds. 2004. Handbook of Ecological Indicators for Assessment of Ecosystem Health, CRC Press, Boca Raton, FL.

Abstract

Indicators were used to estimate wetland divergence and convergence in a whole ecosystem experiment in central Ohio, USA. Two similar-geomorphology, 1-ha flow-through created wetland basins were maintained with similar inflow and water depth for 6 years. One basin was planted with 2,500 individual rootstocks of 13 species of macrophytes at the beginning of the 6-year study; the second basin was left unplanted. Both basins were then subjected to natural additional colonization of plants, algae, microbes, and animals. Macrophyte community diversity was estimated by a new community diversity index (CDI) and this was treated as the independent variable. By the sixth year, CDI diverged in the two wetlands with the "planted" basin supporting several macrophyte communities of mostly introduced species and the "unplanted" or "naturally colonizing" basin dominated by an invasive *Typha* spp. monoculture. With this difference in community diversity came a divergence in ecosystem structure and function. Sixteen indicators of wetland function (dependent variables) were observed annually and relative differences between the wetland basins were determined by a non-parametric similarity index. The basins were ecologically similar through years 3 through 5, but by the sixth year of the experiment, the basins diverged in function with only 44% similarity after similarity between 75 and 87% for years 3 through 5. The macrophyte-diverse wetland that resulted from planting had higher water column productivity, water temperature, dissolved oxygen, and pH. The naturally colonizing *Typha* wetland had higher macrophyte productivity, benthic invertebrate diversity, outflow suspended sediments (turbidity), and dissolved ions (conductivity) . Different bird, amphibian and fish use are also hypothesized as having resulted from the planting and differential colonization. Our large-scale, long-term, whole-ecosystem findings dispute some findings of small-scale, short-term, replicated mesocosm experiments.

Introduction

Few studies have investigated how macrophyte diversity affects ecosystem function in created and restored wetlands, despite the frequent use of macrophyte cover and diversity as determinants of legal and ecological success of these wetlands in mitigating wetland loss, particularly in the USA.[1-5] Engelhardt and Ritchie[6] manipulated seventy 1.5-m diameter wading pools with one, two, and three species of the submersed pondweed (*Potamogeton* spp.) and found that higher algal biomass and higher phosphorus uptake occurred in the pools with highest macrophyte species richness. They concluded that higher species richness created up to 25% higher algal biomass that caused 30% more phosphorus uptake and thus would support more wildlife and fish. They further concluded that a wetland with high richness or diversity due to disturbance might better "sustain ecosystem functioning and promote the services of those wetlands to humans."[6]

Alternatives to the replicated small-scale mesocosms for wetland study are large-scale, long-term whole ecosystem studies that include more components of the ecosystem. Whole-ecosystem experiments, which have been carried out for terrestrial systems, [7-10] lakes,[11-14] and wetlands [2, 15-16] are often criticized because the size, cost, and logistics alone do not allow for much if any replication. Some researchers suggest that there is no single optimum scale for ecosystem experimentation but state that it is easier to apply statistical methods successfully to many small replicated systems. [17-18]

We present here a 6-year, whole-ecosystem wetland experiment that illustrates: 1) the effect of macrophyte introduction and subsequent macrophyte community development on ecosystem function, and 2) the use of simple, easy-to-measure, indicators for assessing large-scale, long-term, whole-ecosystem experiments in wetland ecology. Our study investigates the relationship between macrophyte community diversity and ecosystem function in light of current theories on biodiversity and ecosystem function. Results of this study follow those from the first three years of this study that were previously published.[2] Those early results illustrated that marsh functions in the experimental wetlands diverged and then converged in concert with divergence and convergence of macrophyte development. After 6 years, some of those findings were validated while our conclusion on the time over which introduction of plant diversity has a measurable effect on ecosystem function is now determined to be longer than we originally thought.

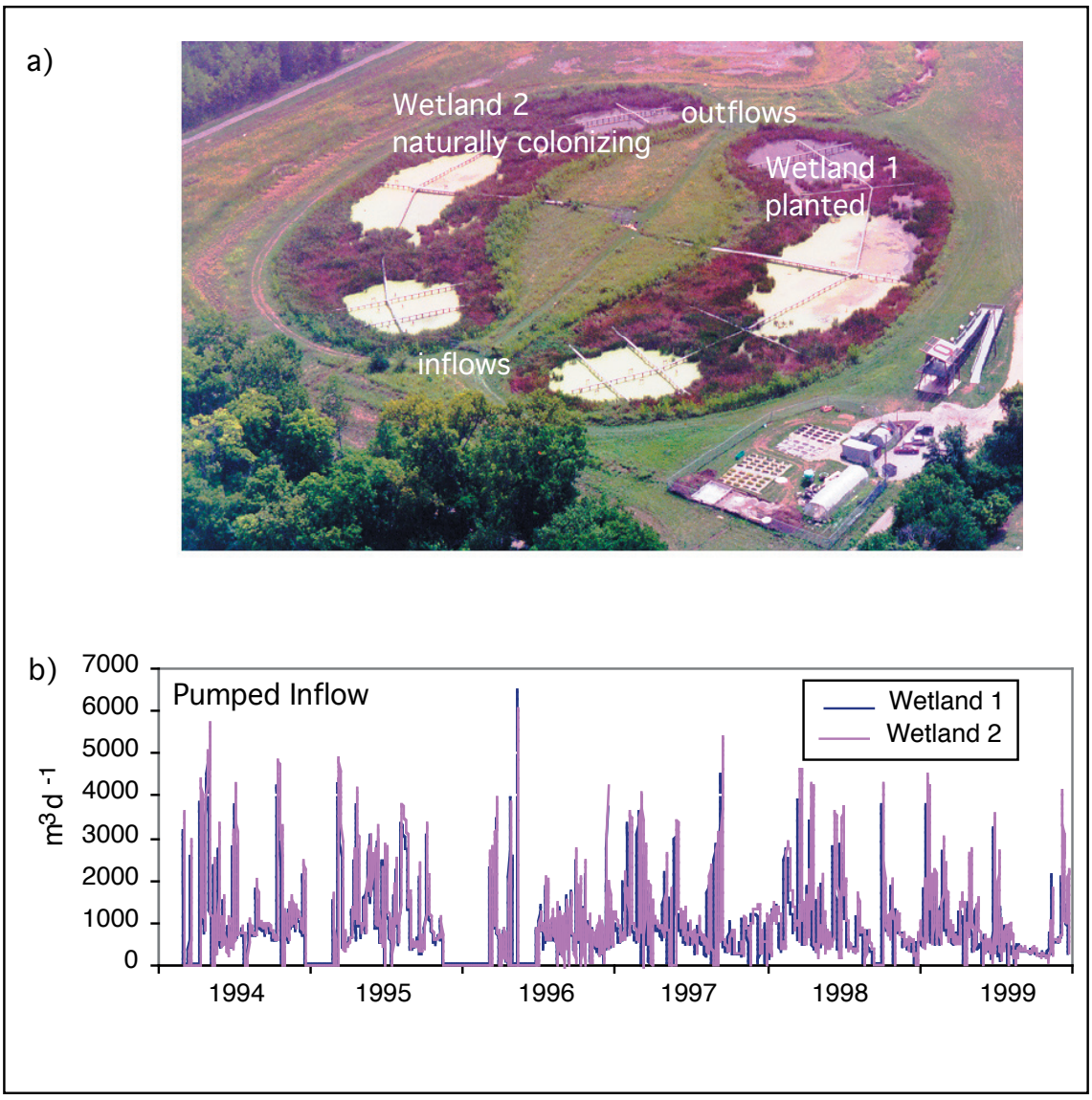

Figure 1. a) Paired 1-ha experimental wetlands at the Olentangy River Wetland Research Park at The Ohio State University (photo in August 1999). Planted wetland basin (W1) is on the right; basin planted by nature (W2) is on the left; b) pumped inflow to planted (W1) and naturally colonizing (W2) wetland basins for the 6 years described here. Water levels and water budgets were essentially identical over the 6-year period discussed here.

Methods

Site history

Two 1-ha experimental wetlands and a river water delivery system were constructed in 1993-94 at The Olentangy River Wetland Research Park, a 10-ha site on the campus of The Ohio State University in Columbus (Fig. 1a). Over 2,400 plant propagules (mostly root stock and rhizomes) representing 13 species typical of Midwestern USA marshes were planted in one wetland (Wetland 1=W1) in May 1994. Wetland 2 (W2) remained unplanted. Both wetlands received the same amount and quality of pumped river water and both have had essentially identical hydroperiods for the entire six-year study period (Fig. 1b). Pumped river water generally flows into the wetlands continuously, day and night, except for planned drawdowns, and occasional short-term unscheduled pump failures. After start-up trials in 1994, a pumping protocol was developed that involves changing the pumping rate manually 2 or 3 times per week according to a formula that calls for more pumping when river discharge is high and less pumping when river flow is low. On an annual average, pumped inflow to each wetland has been 20-40 m/yr. Water depths in the major portions of the wetland are generally 20 to 40 cm in the shallow areas where most of the emergent macrophytes grow and 50 to 80 cm in the deepwater areas that were constructed in the wetland to allow over wintering of nekton and additional sediment storage. Five river flooding events occurred during the study period. During each of these floods, water from the river spilled into the wetlands in approximately equal amounts.

Macrophyte community index

Macrophyte coverage by dominant community is estimated each year from aerial color photography taken at the period of peak biomass (late August), coupled with ground truth surveys. Ground surveys involved mapping plants along 500 m of 7 transects (shown in Fig. 1a) in each wetland. Transect permanent walkways are about 1.5 m above the wetland soil, thus giving a good perspective even with 3 m-tall plants. A 10 m x 10 m grid system marked with permanent numbered white poles is used to identify the location of plant communities in each wetland. Maps for each year are normalized to the same size basin map utilizing geographic information system software.

We developed a macrophyte Community Diversity Index (CDI) to quantify the diversity in the wetland basins. The index used relative areas of macrophyte community cover from the maps derived above and the mathematics of the Shannon-Weaver diversity index, with area of each community instead of number of individuals of each species used. It is expressed as:

$$CDI = - \sum_{i=1}^{N} C_i \ln(C_i)$$

where

C_i = percent cover of wetland community "i" (0 to 1) in the wetland basin

N = number of wetland communities

Overall, there were seven different communities identified by our combination of aerial photography and subsequent ground surveys during the 6-year study. They were named for the dominant species in community:

* *Schoenoplectus tabernaemontani*,
* *Typha* spp.,
* *Scirpus fluviatilis*,
* *Nelumbo lutea*,
* *Sparganium eurycarpum*,
* *Spartina pectinata*, and
* open water/submersed aquatics.

Field indicators

Aboveground biomass during August was used as an estimate of aboveground net primary productivity (ANPP). It was estimated directly beginning in 1997 by direct aboveground harvesting of sixteen 1-m^2 plots in each wetland along sampling boardwalks and from aerial photography and fewer sample plots before that. Algae are sampled several times each year at inflow, middle, and outflow areas in both wetlands with a plankton net tossed 5 m and retrieved with a cord. Samples representative of metaphyton such as attached and benthic algae are taken by hand. Algal species are identified by microscope at 100x and 400x and relative abundance of each genus is estimated. Daily dawn-dusk-dawn readings of dissolved oxygen from manually taken measurements at the outflows are used to estimate aquatic productivity of the water column.[19] More than 60 such paired dawn-dusk samples were available each year. Benthic invertebrates are sampled in late October - early November annually with Hester-Dendy plates (11 cm^2) placed at nine stations in each wetland. Sometimes this sampling has been supplemented with dip net collections and bottle collections. Invertebrates are sorted to lowest recognizable taxa and Shannon-Weaver diversity indices are estimated with these taxa counts. Taxa diversity measures with and without pollution-tolerant organisms (oligochaetes, tubificids, and chironomids) were used as relative indicators in the two wetlands of aquatic community diversity.

Manual sampling of water temperature, dissolved oxygen, pH, conductivity, and redox has been done twice-per-day (dawn and dusk) with Hydrolab H20G or YSI 6000 water quality sondes at the inflow of the wetlands and outflows of both wetland basins. One-hundred mL samples are also taken dawn and dusk each day at the inflow and two outflows for turbidity analyses in the laboratory with a Hach ratio turbidimeter. In addition to the twice-per-day manual sampling, weekly water samples are taken at inflows and outflows of the wetlands for nutrients which were determined by standard methods .[20,21]

Basins were observed for avian activity in the early years through exact walking paths by experienced observers several times during the year. Comparison of avian use of

the basins in 1999 was made through frequent visits to the basins in spring. Bird presence is noted by both songs and sightings.

Similarity index

Basins were compared yearly by using 16 indicators, listed in Table 1 and described above, that represent the structure and function of the wetland ecosystems. We used one indicator of macrophyte function (aboveground net primary productivity), four indices of aquatic community development (two macroinvertebrate diversity indices, aquatic GPP, and algal species richness), six indicators of wetland biogeochemistry (outflow concentrations of pH, conductivity, redox, turbidity, dissolved oxygen, and temperature), three indicators of nutrient retention (SRP, total P, and nitrate-nitrogen retention), and two indicators of avian use (bird abundance and species richness) in each wetland basin. The non-parametric similarity of each basin was estimated with a similarity index (SI) calculated as:

$SI = [I_S / I] \times 100$

where

SI = similarity index

I_S = number of similar functional indicators in a given year

I = total number of functional indicators = 16

Results

Macrophyte community diversity

Emergent macrophyte communities developed in both wetlands to the point where almost all of the available shallow water area was vegetated by the end of the fourth growing season (Table 2). Vegetation appeared to converge by the third year with each basin dominated by *Schoenoplectus tabernaemontani* but with some presence of naturally colonizing *Typha* in each basin. *Typha* spp., a clonal dominant, was not planted but was seen in both wetlands approximately 3 months after the 1994 planting. In the first year of convergence, 1996, *Typha* actually had slightly greater cover in the planted W1 (Fig. 2a). By 1997 (fourth year) it began to develop at a more rapid rate in W2 and by 1999 it has increased to 56% in basin W2 while it remained only 9% cover of basin W1. At this point all shallow areas in W2 were almost completely dominated by *Typha* sp. Similar areas in W1 in 1999 were dominated by communities in the following order from most to least dominant :

Sparganium eurycarpum > *Schoenoplectus tabernaemontani* > *Typha* sp. > *Scirpus fluviatilis*.

Macrophyte species richness increased dramatically in years 3 and 4 to almost 100 species in both basins (Fig. 2b). Species richness proved not to be a useful metric for comparing the two basins. When the wetlands are viewed in terms of plant cover using our community diversity index (CDI), which includes indications of evenness of plant cover as well as number of dominant communities, a different conclusion about macrophyte community diversity is reached (Fig. 2c). The data show two years of basin divergence. The first year of divergence was in year 2 when W1, the planted basin, had 13% plant cover but W2 had no macrophyte development. The second macrophyte community divergence occurred in the sixth year (1999) when, after 3 years of similar plant cover in the two basins, different spatial community diversity developed. The CDI in W2 dropped as *Typha* formed close to a monoculture while it increased in W1 as a good balance among 5 communities developed, with 4 of those communities dominated by plants introduced in the planting (Fig. 2c; Table 2).

Macrophyte productivity

Productivity ranged from 657 to 729 g m^{-2} yr^{-1} in W1 and 756 to 1127 g m^{-2} yr^{-1} in W2. In the first year that macrophyte above-ground net primary productivity (ANPP) was measured by our standard techniques (1997; fourth year of the study) it was statistically similar in both basins (Fig. 3a). ANPP was statistically higher ($\alpha = 0.05$) in W2 in both year 5 (1998) and year 6 (1999) due to the dominance of the highly productive *Typha* that covered 43 and 56% of W2 in those two years respectively.

Algal development

Dense benthic and floating metaphyton were significant in both wetlands throughout the study because of more than adequate nutrient concentrations in the inflowing river water. In the first year, large metaphyton mats developed in both basins; these mats were composed of *Hydrodictyon reticulatum* (L) Lag. and *Rhizoclonium* spp. along with extensive epiphytes of several species of Chlorophyta and Chrysophyta.[22] In the second year, the planted wetland (W1) carried an average of 80% of all of the genera identified while the unplanted wetland (W2) supported less (70% of those genera). By the third year (1996), that statistic was 79% for W1 and 74% for W2, illustrating some convergence. The apparent increase in algal diversity in W2 in the third year correlated with the natural colonization of macrophyte cover .[2] Macrophytes may have increased habitats for the microphytes. By the fifth year (1998), the deepwater areas in the two wetlands started to become dominated by *Lemna minor*, causing dramatic decreases in metaphyton during some periods. Although there have been some differences in the two basins in 1998 and 1999, it appears that there has been general convergence of algal species since year 3 (1996).

Gross primary productivity (GPP) in the water column, as a functional measure of algae and submersed aquatic communities, was generally inversely related to macrophyte productivity (Fig. 3b). When productivity of macrophytes was different between the two wetland basins, as was the case in the second (1995) and fifth (1998) and sixth (1999) years, GPP in the water column compensated by being higher in the basin with lower macrophyte productivity. When there were

Table 1. Indicators of ecosystem structure and function used to compare experimental 1-ha wetlands at Olentangy River Wetland Research Park, 1994-99.

Indicator	Ecosystem Structure or Function
I. macrophyte community function	
1. net aboveground primary productivity	macrophyte community organic production
II. aquatic community development	
2. algal species richness	water column diversity
3. aquatic metabolism	water column organic production
4. macroinvertebrate diversity	benthic biodiversity
5. “clean water” species richness	balance of P and R
III. biogeochemistry	
6. temperature change	shading of water column
7. turbidity change	sedimentation/resuspension
8. dissolved oxygen change	oxidation/reduction
9. pH change	CO_2 uptake/release in water
10. specific conductance change	chemical precipitation/absorption
11. redox change	oxidation/reduction balance
IV. nutrient dynamics	
12. total phosphorus change	phosphorus retention
13. soluble reactive phosphorus change	phosphorus microbial uptake
14. nitrate+nitrite change	denitrification/nitrogen retention
V. Avian use	
15. abundance	food source/habitat abundance
16. species richness	food source/habitat richness

Table 2. Coverage (m^2) in each basin by dominant vegetation communities, 1994 -1999.

Zone (m^2) that are dominated by	1994		1995		1996		1997		1998		1999	
	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2	W1	W2
Total basin	8903	8672	8903	8672	8903	8672	8903	8672	8903	8672	8903	8672
Community												
Open water	1451	2567	7746	8672	5333	5498	3579	3035	3490	2567	3276	2914
Algal mat	7452	6105										
Schoenoplectus tabernaemontani			1157		3205	3018	4149	4163	3668	2333	1914	876
Typha spp.					365	165	445	1440	98	3772	792	4882
Scirpus fluviatilis							205		392		258	
Nelumbo lutea/Potamogeton sp.							107	35	89			
Sparganium eurycarpum						418			1166		2261	
Sagittaria latifolia							9					
Spartina pectinata											401	
Total-rooted macrophytes	0	0	1157	0	3570	3661	4915	5638	5413	6105	5626	5758
% macrophyte cover	0	0	13.0	0	40.1	42.2	55.2	65.0	60.8	70.4	63.2	66.4

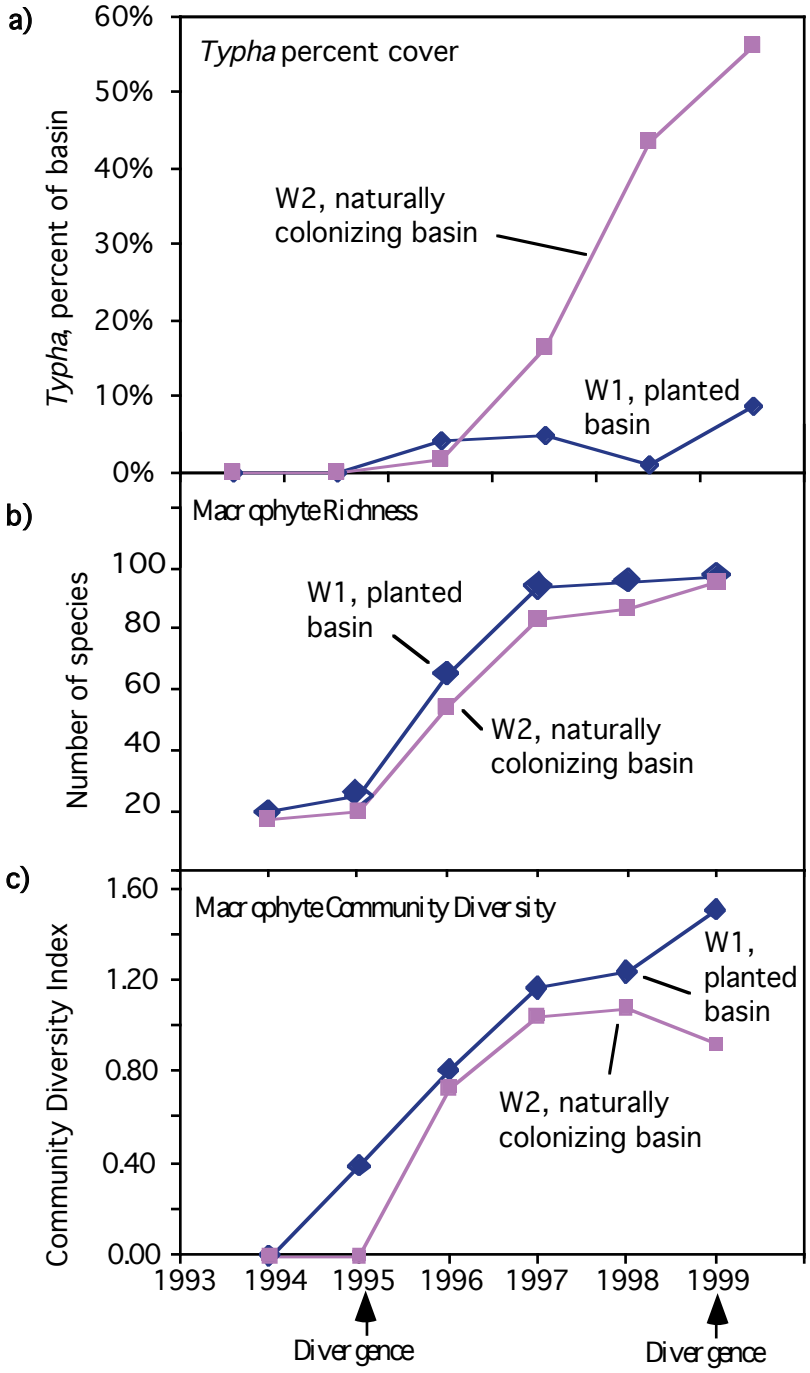

Figure 2. Indicators of macrophyte diversity in the two experimental wetlands, 1994-99: a) Percent of cover that is *Typha* spp.; b) macrophyte species richness; and c) macrophyte community diversity index (CDI). Note divergence of macrophyte community diversity in 1995 (year 2) and in 1999 (year 6).

considerable macrophytes in the planted W1 but not in the unplanted wetland (W2) in the second year, water column GPP was higher in the unplanted wetland W2 by 38%. The situation reversed in 1999 when statistically higher water column GPP occurred in the planted wetland (W1) than in the naturally colonizing wetland (W2), consistent with the greater macrophyte biomass cover in W2.

Macroinvertebrate Diversity

Macroinvertebrate taxa diversity remained statistically similar from 1996 through 1998 when plant communities were well developed but similar in both wetlands (Table 3). Taxa diversity diverged in 1999 when *Typha*-dominated W2 had a statistically higher benthic invertebrate diversity. Except for the first two years of wetland development, clean water species richness and diversity (count and diversity of all taxa minus chironomids, oligochaetes, and tubificids) were generally similar in both wetlands (Table 3).

Water chemistry

Water chemistry changes as the water flowed through the wetlands showed several differences between the two wetlands in certain years and for certain parameters (Fig. 4). In the sixth year, 7 of 9 parameters were different from inflow to outflow in each wetland ($\alpha = 0.05$) and the wetlands were different from one another ($\alpha = 0.05$) in 5 of 9 water quality parameters. Changes also occurred from year to year as macrophyte cover developed and began to influence water quality. For example, temperature increased through the wetlands on average in each of the first 5 years, but the increase was less each year (Fig. 4a). By the sixth year (1999), temperature actually decreased on average as water flowed through the wetlands and was also statistically different in the two basins after two years of convergence. Average dissolved oxygen (daily average of dawn and dusk readings; Fig. 4b) was initially different in the two basins (1994 and 1995) and increased by 30 to 45 % through W2, which did not have any macrophytes shading the water during this period. When macrophytes developed in the basins, as they did from 1995 in W1 and from 1996 in W2, dissolved oxygen increased by 25% or less. Dissolved oxygen increase was higher in the planted W1 in 1999 after 3 years of similarity. pH (Fig. 4c) was significantly different in the two wetlands during four of the six years. It increased more in the then-unvegetated W2 than in the planted W1 in the early years (1994 and 1995). This pattern reversed in later years when W1 had significantly higher pH than the naturally colonizing wetland W2 in years 5 and 6 (1998 and 1999). Conductivity changes (Fig. 4d) were significantly different between the two wetlands during the second year and in the final 3 years. Conductivity decreased more in the then-unvegetated W2 in 1995. Then the pattern switched, with conductivity decreasing more in the planted W1 than in W2 in 1997 through 1999. The pattern also showed that, except for the first year, there was generally less change in conductivity through the wetlands with each succeeding each year as macrophyte vegetation developed. Turbidity, as a measure of suspended materials that include allochthonous clay and silt particles and autochthonous algal cells, decreased through the wetland every year (Fig. 4e). Changes through the two wetlands were different in the second (1995) and sixth (1999) years, the same two years in which the macrophyte diversity (CDI) diverged. In 1995 turbidity decreased more in the planted W1 than in the still-unvegetated W2. In 1999, turbidity also decreased more in the diverse wetland W1 than in the Typha monoculture W2. Redox potential (Fig. 4f) in the outflow water has not differed much in the two wetlands except early in the study. It also appears that redox potential is decreasing more each year in both wetlands' outflows. In 1997 redox potential was essentially unchanged from inflow to outflow. In 1999 it decreased on average between 6 and 7 percent.

Nutrient retention

Nutrient (phosphorus and nitrogen) reduction was consistent and significant in both wetlands throughout the six years for the three nutrient species analyzed (Fig. 5). Total phosphorus concentration annual reductions ranged from 18 to 73% per wetland and there appears to be a trend of less total phosphorus retention each year. Percent reduction of soluble reactive phosphorus (SRP) through the wetland basins has been higher (50 to 90% removal) and more consistent than that of total phosphorus . Percent reduction of nitrate+nitrite-nitrogen has remained consistent from year to year (generally between 20 and 50% reduction) in each wetland. Decreases from inflows to outflow have been significantly different for both wetlands and all years ($\alpha = 0.05$). There were few statistically significant differences in nutrient retention between the wetlands over the six-year study with only two differences out of a possible 18 parameter-years.

Avian use

A total of 150 bird species were identified at the Olentangy River Wetland Research Park from 1992-99 with a 20% increase in species richness in the first year after wetland construction, another 8% increase during the second year, and an additional 5% increase in the third year. The creation of the wetlands resulted in the addition of about 35 wetland-specific bird species to the site. Because of the proximity of the two wetlands, it has been generally difficult to compare avian use of the two wetlands. Nevertheless, surveys in the second year and reported previously did find that the planted W1 consistently supported a greater number of species (nesting and migratory) and more individuals than did the unplanted W2.[2] Two species in particular, the sora (*Porzana carolina*) and marsh wren (*Cistothorus palustris*), were found exclusively in the planted wetland in the second year. By the third year, with the development of vegetation cover in the unplanted W2, differential bird use between the two wetlands declined and similar numbers and richness of species were found in each. With the development of different macrophyte communities in 1999 in the two

wetlands, differences in bird use between the basins were observed (Fig. 6). There were significantly greater numbers of red-winged blackbirds (*Agelaius phoeniceus*) in W2 and significantly greater numbers of song sparrows (*Melospiza melodia*) in W1. Red-winged blackbirds have a great affinity for *Typha* while song sparrows favor the less dense vegetation in wetland W1.

Basin similarity

According to our community diversity index (CDI) and similarity index (SI) of wetland structure and function, there were two years out of six where the two wetlands diverged (Table 4; Fig. 7). In the second year (1995) after wetland construction, substantial macrophyte cover developed only in the planted wetland W1 as expected and none was present in W2; therefore the CDI index was different in the two wetlands (it was 0.0 for the unplanted wetland). Only 13% of the ecosystem indicators were similar (SI = 13%). In years 3, 4, and 5, the macrophyte CDI was similar between the two wetlands and the ecosystem similarity converged to 75 - 87%. *Typha* invasion into the unplanted wetland in the sixth year (1999) caused a second divergence in the CDI between the two basins (Fig. 3c) and wetland function diverged a second time (Fig. 7). During this year the similarity of the two wetlands dropped to 44%.

The similarity index between the two wetlands for each year is plotted versus the difference in the community diversity index (CDI) between the basins for the same year (Fig. 8). The regression ($r^2 = 0.53$) suggests that when the two basins were different in community diversity (as in 1995 and 1999) the two wetlands were dissimilar in structure and function (SI = 13-43%). When the basins were similar in community diversity, the two basins were similar in structure and function (SI = 70-88%).

Discussion

Community diversity and ecosystem function

Our study suggests that structure and function are related to macrophyte community diversity in wetlands. In years when macrophyte community diversity was similar between our two wetlands, ecosystem indicators were also similar. When wetlands had different macrophyte community diversity, structure and function were different. Our macrophyte community diversity index (CDI) is not a traditional species diversity of small managed plots but rather is a measure of the spatial diversity that can be seen from good aerial photography. It includes both the richness and evenness of communities patterns.

When aboveground net primary productivity is plotted versus CDI for 6 wetland-years, a negative relationship (Fig. 9). When the macrophyte community is diverse in terms of spatial patterns. While our study uses a measure of spatial community diversity (the diversity of pixels in a color map) and other studies count individual plants or stems, some comparison can be made between our general findings and those suggested by others on the relationship between productivity and diversity. Plot and small-scale terrestrial research often illustrates that plant diversity has a positive effect on primary productivity. While this may hold true for managed diversity of plants on small plots, our results show exactly the opposite for large-scale wetlands. Higher diversity on a community scale (that is, how many different macrophyte communities are present and how even their distribution is) not only does not enhance productivity, our study suggests that it reduces it. This tempers the universality of conclusions suggested by studies in grasslands[27,28] and more recently for mesocosm wetlands[6] that diversity enhances productivity. These studies were carried out on smaller scales than ours and were also subject to some manipulation to maintain certain diversities. [23,24]

There was no significant relationship seen in our study between community diversity index (CDI) and gross primary productivity of algal communities ($r^2 = 0.004$) or nutrient and sediment retention (phosphorus: $r^2 = 0.017$; nitrates: $r^2 = 0.004$; turbidity: $r^2 = 0.05$). This last lack of a significant relationship is in direct conflict with the conclusion by Engelhardt and Ritchie[6] that "higher vascular plant richness in wetlands may potentially yield up to 25% more algal biomass….and retaining (sic) up to 30% more potentially polluting nutrients, such as P." While these conclusions may be applicable to small-scale experiments they were not supported by our full-scale wetland ecosystem study.

Productivity as the independent variable

We suspect that asking what the effect is of diversity on productivity may be the wrong question to ask, as ultimately physical and chemical factors affect productivity, which in turn often determine biodiversity which feedbacks and affects the physics and chemistry. If we turn the cause and effect around by rotating Fig. 9 ninety degrees, we have illustrated what is already fairly well established in the wetland literature [25-27] that species richness and diversity in freshwater marshes and lakes are inversely related to biomass and productivity. Productivity in turn is related to factors such as nutrients, sunlight, and flooding. When primary productivity is viewed in this way as the independent variable, then several ecosystem functions which do not correlate well with macrophyte community diversity, correlate much better with marsh net primary productivity. Total phosphorus, nitrate-nitrogen, and to a lesser degree, turbidity reductions are positively related to ANPP (Fig. 10). Although long suspected, there has been no study to our knowledge that has confirmed this relationship at a full-ecosystem scale. Tanner[28] found a relationship between biomass (productivity) and nitrogen uptake similar to the one we did between ANPP and nitrogen retention. His New Zealand study involved gravel-bed mesocosms fed by high-concentration dairy wastes. Therefore, nitrogen concentrations were substantially greater in his study than ours. Experiments in Norway[29] involving 4 small wetlands showed that suspended sediment retention increased with

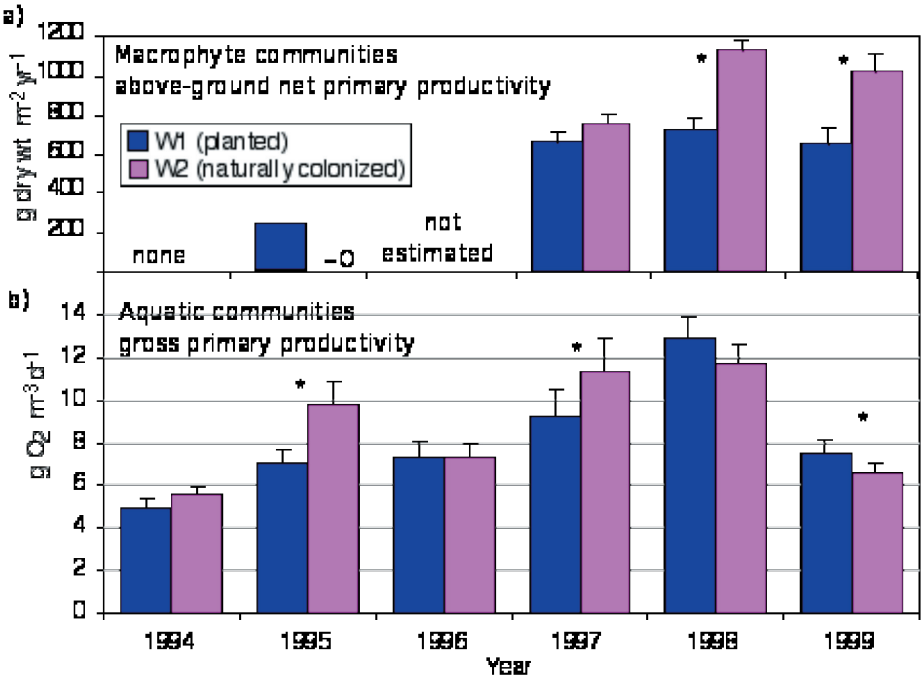

Figure 3. a) Macrophyte net aboveground primary productivity (NAPP) in grams dry weight and b) aquatic community gross primary productivity (GPP) in grams O_2 of two experimental wetlands. Asterisk (*) indicates significant difference between wetlands (α = 0.05). Macrophyte NAPP was not estimated during the first 3 years by harvesting because of the feared impact that would have on the experiment when vegetation was just starting. Vegetation was different in 1995 because there were essentially no macrophytes in W2 in that year while the planted macrophytes covered 13% of W1.

Table 3. Benthic invertebrate diversity in two experimental wetlands, 1994-1999

Year	Total count diversity index		"Clean water" diversity index	
	W1	W2	W1	W2
1994 (planting)	0.63	0.69	0.45	0.60
1995 (divergence)	0.50	0.62	0.98	0.51
1996 (convergence)	0.88	0.83	0.88	0.86
1997 (convergence)	1.34 ± 0.02	1.41 ± 0.18	1.23 ± 0.28	0.96 ± 0.17
1998 (convergence)	0.58 ± 0.43	0.82 ± 0.56	0.58 ± 0.43	0.73 ± 0.45
1999 (divergence)	0.63 ± 0.05*	0.91 ± 0.12*	0.49 ± 0.13	0.61 ± 0.17

Indices are Shannon-Weaver index

W1 = planted wetland; W2 = natually colonizing wetland

"Clean water" = all taxa execpt chironomids, oligochaetes, and tubificids

*Significant differences (α = 0.10) between wetlands from last 3 years for paired samples. Earlier years' data indicate overall diversity indices for entire wetland basin.

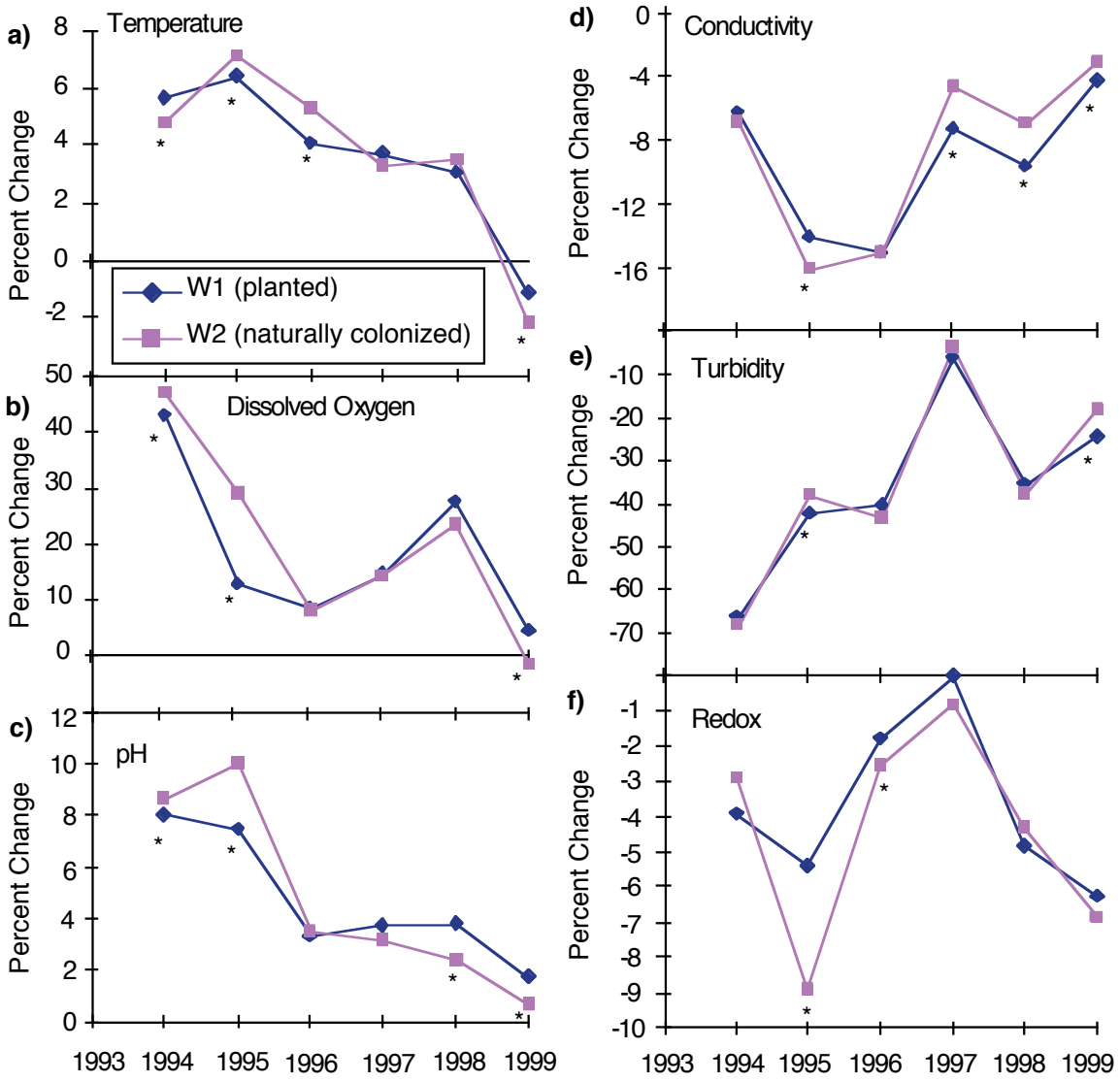

Figure 4. Water quality changes through experimental wetlands for 1994-99: a) temperature; b) dissolved oxygen; c) pH; d) conductivity; e) turbidity; f) redox potential. Data points indicate overall percent change from inflow to outflow of averages of all inflow and outflow concentrations during that year. Each data point represents hundreds of samples per year. Asterisk (*) indicates significant difference between the wetlands as determined by t-test comparing outflow concentrations (α = 0.05).

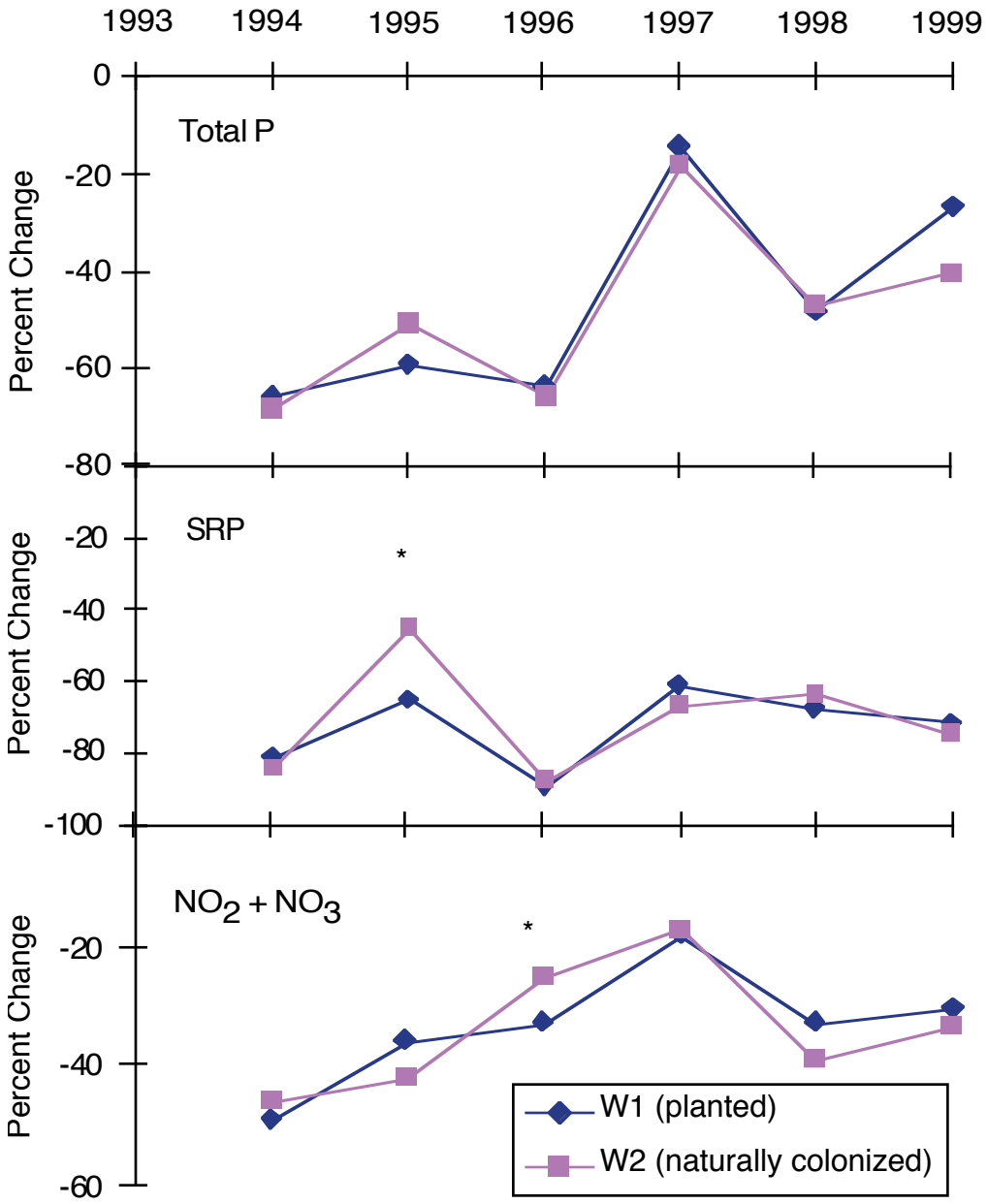

Figure 5. Nutrient retention in the two experimental wetlands for 1994-99: a) total phosphorus (Total P); b) soluble reactive phosphorus (SRP), and c) nitrite + nitrate nitrogen ($NO_2 + NO_3$). Data points indicate overall percent change from inflow to outflow of averages of all inflow and outflow concentrations. Each data point represents overall results of weekly readings over a year. Asterisk (*) indicates significant difference between the wetlands as determined by t-test comparing outflows ($\alpha = 0.05$).

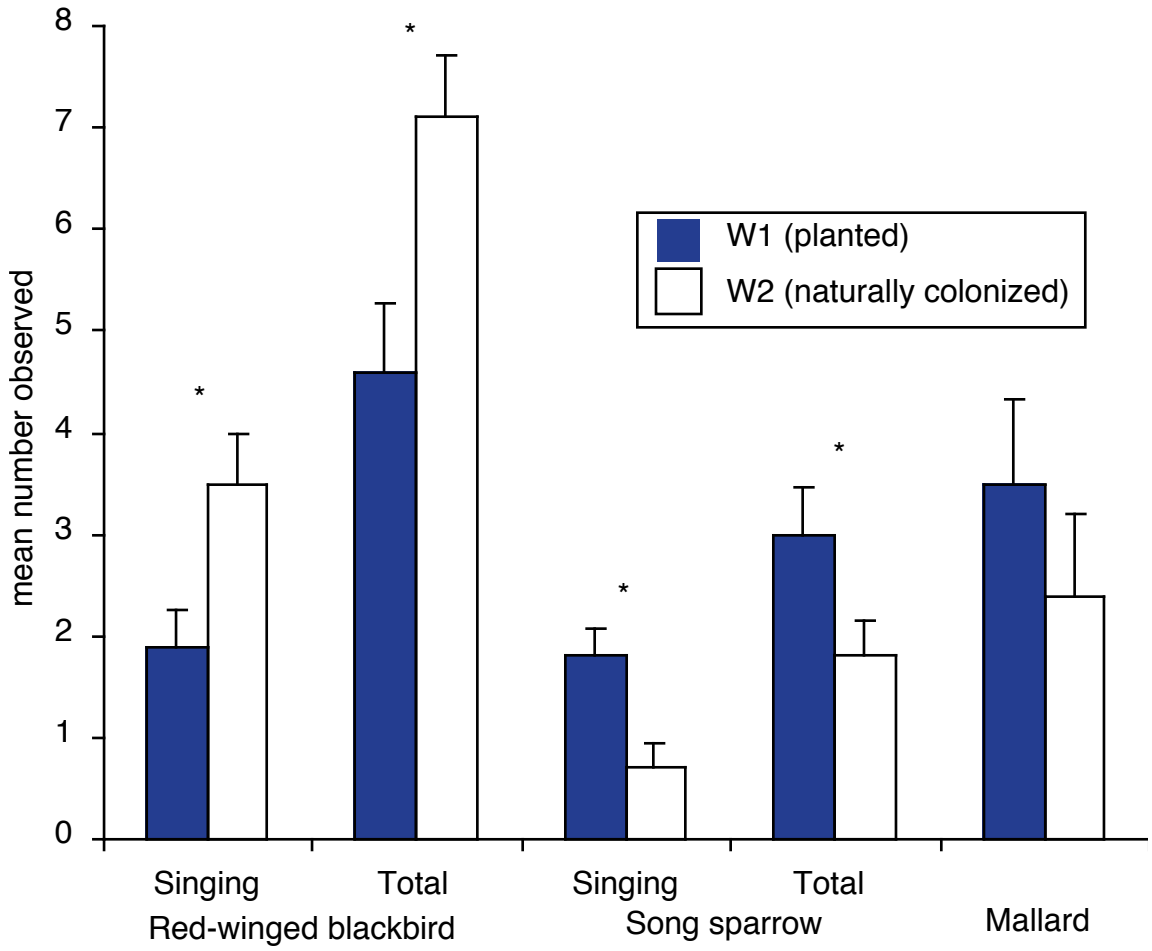

Figure 6. Bird observations comparing the two experimental wetlands in 1999. Asterisk (*) indicates significant difference between wetlands (α = 0.05).

greater vegetation cover, not so much because of any increase in sedimentation but because of a reduction in resuspension. Factors such as this are a more likely explanation for the Fig. 10 patterns than any direct uptake by the macrophytes.

Diversity at different levels

It is often assumed that if one trophic level of an ecosystem is diverse, that diversity will "spill over" to other parts of the ecosystem. This is a structure affecting structure argument and is partially the theory of consumer control of species diversity.[30] The effect of macrophyte community diversity on benthic invertebrate diversity was compared for 1997-99 (3 wetland-years; Fig. 11) in the same fashion as the macrophyte comparison above. There was a weaker inverse relationship ($r^2 = 0.23$) than that for the effect of macrophyte productivity on invertebrate diversity ($r^2 = 0.43$). Macrophyte community diversity does not appear to necessarily increase benthic diversity; in fact our data suggest that in some cases it reduced it.

Aquatic consumers

Aquatic consumers were sampled in the wetlands immediately after the year 6 divergence in macrophyte community diversity. There were more *Rana catesbeiana* (bullfrog tadpoles), *Nerodia sipedon* (northern water snakes) and *Lepomis cyanellus* (green sunfish) in the naturally colonizing wetland (W2) than in the planted wetland (W1) in the early 2000 sampling (Table 5). The greater abundance of tadpoles (which consume detritus and small insects) and snakes (which consume tadpoles) suggests a more powerful detrital food chain in W2 in early 2000 that is supported by the macrophyte net primary productivity that was almost 50% higher there in 1999 than in W1. Green sunfish, a species common in wetlands because of its tolerance for warm summer temperatures, may also have been more abundant in W2 because of slightly cooler temperatures (water temperature was significantly cooler in W2 in 1999) caused by the higher macrophyte productivity which, in turn, provides more shade of the water. Greater macrophyte productivity also provides more locations for hiding from predators, including wading birds. The comparison between the wetland basins on fish populations should be made with caution as mark and recapture studies later in 2000[31] showed significantly higher fish populations in W1 after vegetation in both wetlands was lost by a muskrat eatout.

Replication and experimental scale

Whole ecosystem studies, such as the one being conducted here, can provide useful comparisons of ecosystem functions when performed over a long period, even when replication is not possible due to the large size of these systems. We believed that 1 ha was of sufficient size to provide development of all potential ecosystem engineers including ducks, geese, frogs, snakes, and muskrats. C. Korner (conference communication) has made the case for more understanding and acceptance of large-scale experiments and observations in the literature, if for no other reason than that they are a necessary check on theories being published from smaller-scale studies chosen primarily because of elegant replications and statistics. Experiments at small scales allow us to have confidence in the ecological function of small-scale systems. We consider the conclusions of research such as those by Engelhardt and Ritchie's wading pool study[6] on wetland macrophyte richness effects on wetland function as a major overreach given the limitations of small experiments representing full-scale ecosystem function. Using the appropriate experimental scale for extrapolating to the scale of ecosystem function is essential.[32] The large size of the experimental ecosystems and the long period of the study compensates to some extent for the lack of replication. The insights of diversity and ecosystem function would not have manifested themselves in a short-time, small-scale experiment. Many of our findings from this large-scale experiment illustrate that cause and effect on the role of diversity and function may be the reversed of what is postulated in many previous studies.

Carpenter et al.[18] suggest that rather than having an unreplicated experiment, one could actually have two or more similar ecosystems, each with different management or experimental schemes. In our case, we have two large wetland basins, each different means of plant propagule introduction—one by humans and nature and the other by nature. So in effect there is not a control where propagules are weeded or otherwise prevented from entering the wetlands. When one wetland became dominated by *Typha* and the other was not, we were in a good position to see the effects of *Typha* invasions and natural reduction in plant diversity. We believe that use of many physical, chemical, and biological indicators gives strength to our arguments that the basins are similar or dissimilar in any given year.

Specific to this wetland experiment, we[33] compared one of the full-scale 1-ha wetlands with ten 1-m^2 mesocosms in similar hydrologic conditions. While the mesocosm results had statistical rigor because of replication, they had so many scale effects and ecosystem simplifications as to prevent conclusions from being extended to large-scale wetlands without verification with full-scale wetlands. Mesocosm-scale wetlands could not duplicate hydrodynamic features and lacked important aspects of full-scale wetlands such as wind mixing. Also, mesocosm studies of wetlands do not include proportional scales of ducks, geese, muskrats, beavers, and wading birds, all of which can be important "ecosystem engineers" of wetland function.[26, 34-35]

We believe that our 1-ha wetlands, with the large area for all processes to manifest themselves in time and space, are inherently less variable and thus require far fewer replications. As suggested by Carpenter et al.,[18] we believe that there is no optimal scale for ecosystem experiments. But if we desire a system that equally can grow macrophytes, algae and invertebrates in the water column, and at the same time allow for a complete food web including ducks, wading birds, muskrats, and other important parts of any natural wetland, an experiment at 1-ha scale is much more likely to yield true ecosystem functions than would hundreds of

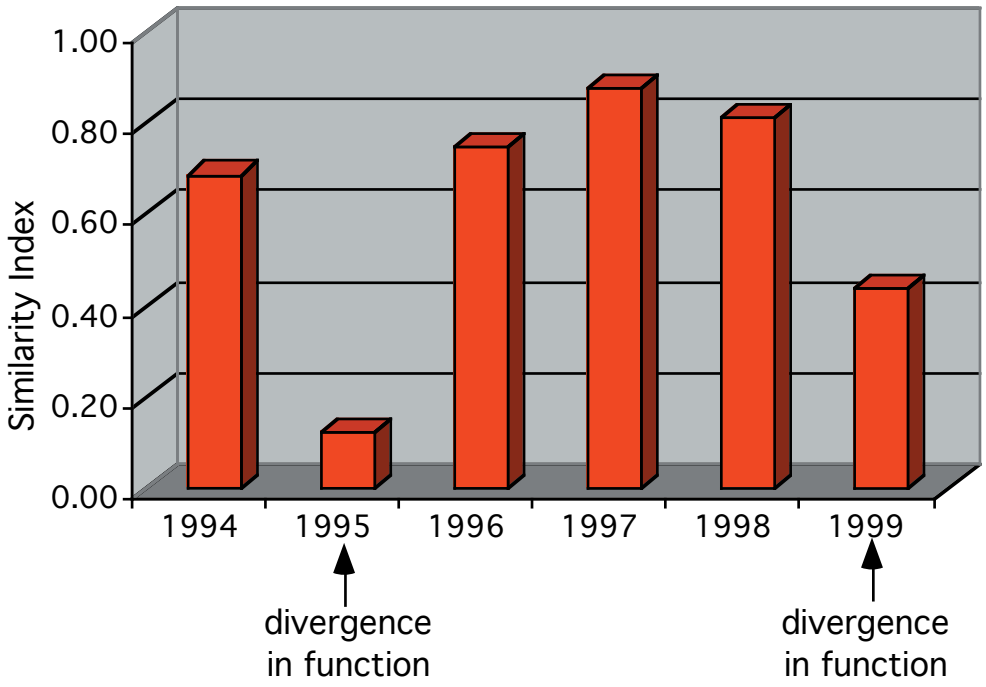

Figure 7. Indicators or similarity between two experimental wetland basins, 1994-99.

Table 4. Summary of 16 indices comparing Wetland 1 (W1) and Wetland 2 (W2) for 6 years, 1994-99

	1994	1995	1996	1997	1998	1999
Macrophyte Diversity, CDI	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2	W1>W2
I. Macrophyte Community Function						
NAPP	W1=W2	W1>W2	W1=W2	W1=W2	W1<W2	W1<W2
II. Aquatic Community Development						
Algal species richness	W1=W2	W1>W2	W1>W2	W1=W2	W1=W2	W1=W2
Aquatic metabolism	W1=W2	W1<W2	W1=W2	W1<W2	W1=W2	W1>W2
Benthic invertebrate diversity	W1=W2	W1<W2	W1=W2	W1=W2	W1=W2	W1<W2
Clean Water species richness	W1<W2	W1>W2	W1=W2	W1=W2	W1=W2	W1=W2
III. Biogeochemistry						
Temperature	W1>W2	W1<W2	W1<W2	W1=W2	W1=W2	W1>W2
Turbidity	W1=W2	W1<W2	W1=W2	W1=W2	W1=W2	W1<W2
Dissolved Oxygen	W1<W2	W1<W2	W1=W2	W1=W2	W1=W2	W1>W2
pH	W1<W2	W1<W2	W1=W2	W1=W2	W1>W2	W1>W2
conductivity	W1=W2	W1>W2	W1=W2	W1>W2	W1<W2	W1<W2
redox	W1=W2	W1>W2	W1>W2	W1=W2	W1=W2	W1=W2
IV. Nutrient Dynamics						
Total P	W1<W2	W1=W2	W1=W2	W1=W2	W1=W2	W1=W2
SRP	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2	W1=W2
NO_3+NO_2	W1=W2	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2
V. Avian Use						
Bird abundance	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2	W1<W2
Bird species richness	W1=W2	W1>W2	W1=W2	W1=W2	W1=W2	W1=W2
Similarity Index, %	69	13	75	87	81	44

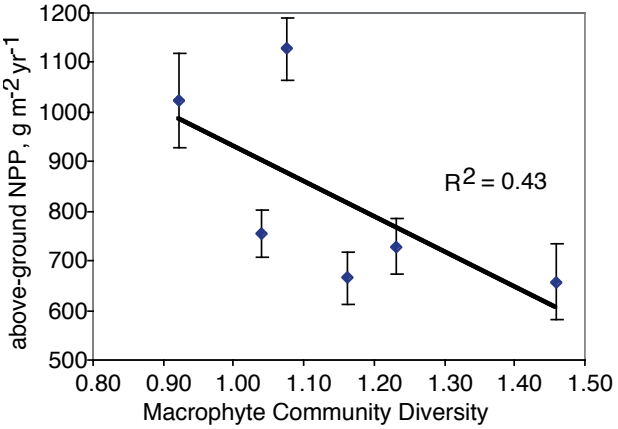

Figure 9. Relationship of aboveground net primary productivity (ANPP) to macrophyte community diversity index (CDI). Each data point is one of two 1-ha basins for years 1997-99.

1-m^2 mesocosms. The use of easily measured multiple indicators allowed us to have more confidence in our relative comparison of these large-scale experimental units than if we relied on only a few indices.

Acknowledgements

We were assisted by many others in this multi-year study including Changwoo Ahn, Virginie Bouchard, Charles Boucher, Randy Bruins, Lesley Carmichael, Melanie Ford, Scott Frazier, Amiei Gifford, Sarah Harter, Cheri Higgins, Megan Hunter, Anne Johnson, David L. Johnson, Sharon Johnson, John Kantz, Katie Kleber, Michael Liptak, Kathy Metzker, Tony Minamyer, Holly Montgomery, Robert Nairn, Uygar Özesmi, Jeff Pearcy, Doug Spieles, Lisa Svengsouk, Rachael Thiet, Paul Weihe, and Renée Wilson. Also appreciated are a number of other students and volunteers who helped with the two-per-day and weekly sampling and laboratory work. This research was made possible by funding from Mid-American Waste Systems, Inc. Ohio Agricultural Research and Development Center, and several other private and public sources. Olentangy River Wetland Research Park Publication Number 2004-05.

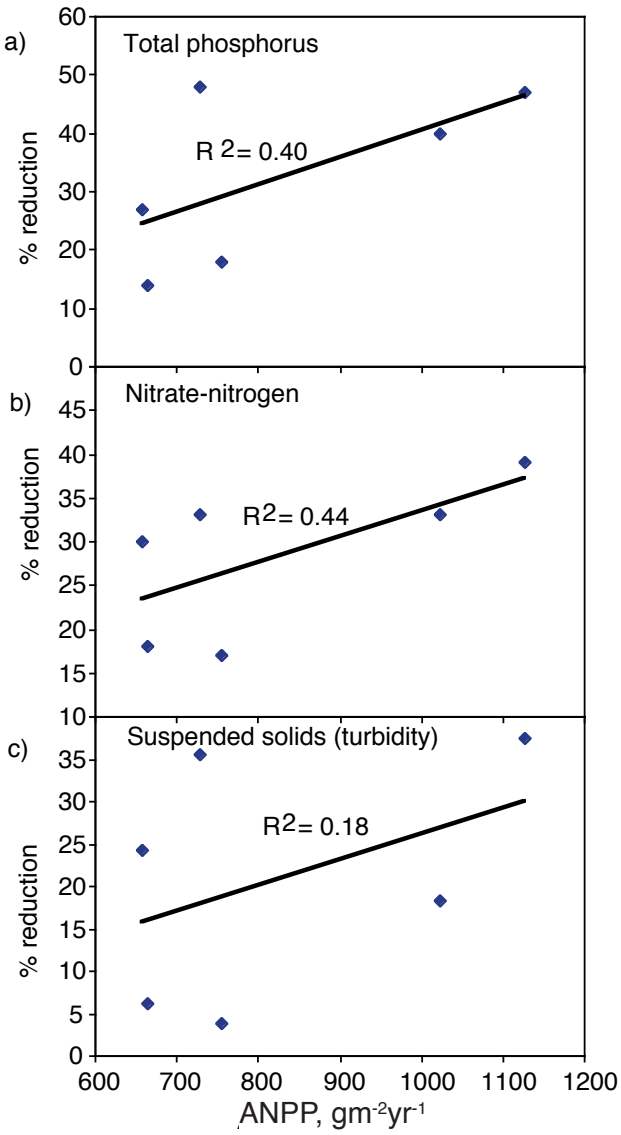

Figure 10. Relationship between nutrient reductions for a) total phosphorus, b) nitrate-nitrogen, and c) suspended solids (measured as turbidity) as a function of aboveground net primary productivity (ANPP) of macrophytes.

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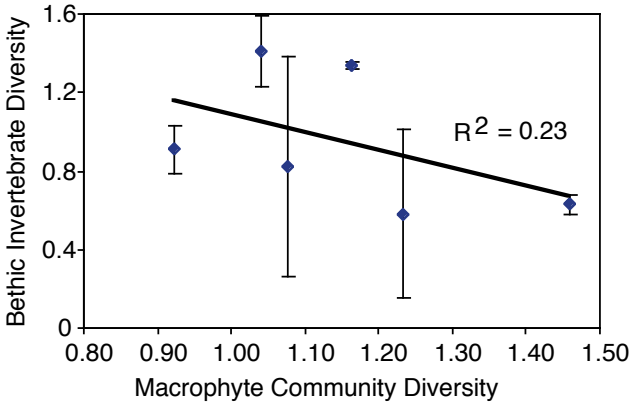

Figure 11. Relationship of benthic invertebrate diversity to macrophyte community diversity index (CDI). Each data point is one of two 1-ha basins for years 1997-99.

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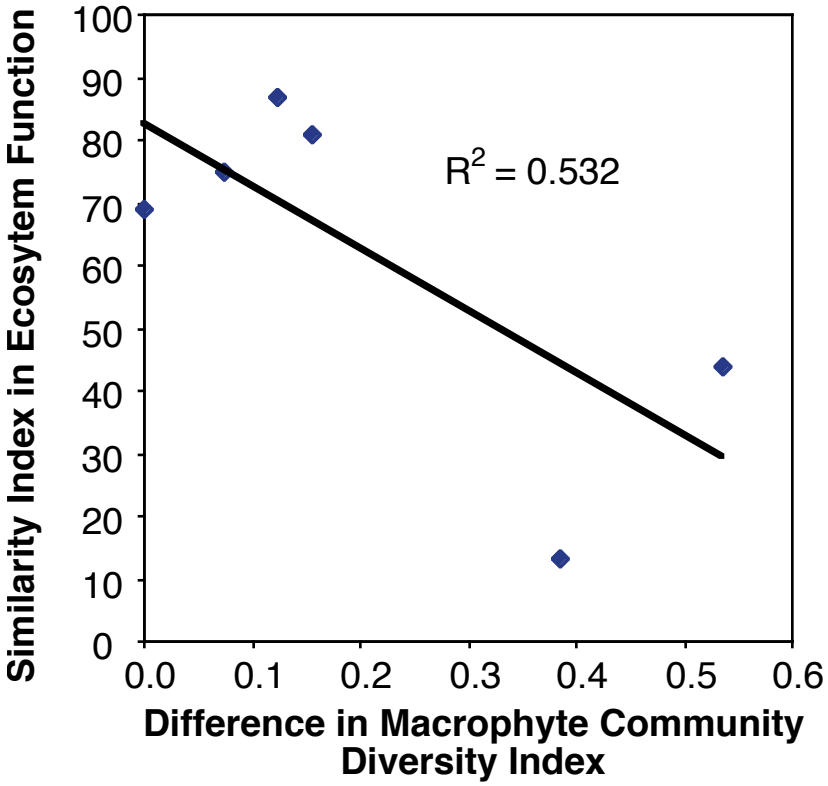

Figure 8. Plot of ecosystem function similarity index (SI) between the two wetlands versus difference in macrophyte community diversity indices (CDI) for the same years. Data illustrate that when the two wetlands were different in CDI, they were also dissimilar in ecosystem function. When wetlands had similar CDI, their ecosystem function was similar.

Table 5. Comparison of amphibians, reptiles, and fish caught in 20 traps in two wetlands in spring of 2000. Numbers are organism caught per trap-day.

Species	Wetland 1 (mean ± S.E.)	Wetland 2 (mean ± S.E.)
Rana catesbeiana	0.015 ± 0.006	0.14 ± 0.024*
Rana clamitans	0.03 ± 0.01	0.02 ± 0.01
Nerodia sipedon	0.006 ± 0.004	0.023 ± 0.008*
Lepomis cyanellus	21 ± 2	34 ± 3*

* indicates significantly higher number compared to Wetland 1 ($\alpha = 0.05$)

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